

# The butterfly assemblages of Onega Lake Area in Karelia, middle taiga of NW Russia (Hesperioidea, Papilionoidea)

VYACHESLAV V. GORBACH<sup>1</sup> & KIMMO SAARINEN<sup>2\*</sup>

<sup>1</sup> Petrozavodsk State University, Department of Zoology and Ecology, RUS-185640 Petrozavodsk, Russia

<sup>2</sup> South Karelia Allergy and Environment Institute, Lääkäritie 15, FIN-55330 Tiuruniemi, Finland

\* corresponding author, e-mail: all.env@inst.inet.fi

**Summary.** The species composition and abundance of butterflies were studied on the north-western coast of Lake Onega in four years (1992–1993, 1995–1996). A total of 50 species and 3,832 individuals were observed during 1,554 transect counts at 111 sites. The most abundant species were *Callophrys rubi*, *Brenthis ino* and *Pieris napi*. The abundance of the majority of species was rather similar compared to the adjacent provinces of Russian and Finnish Karelia. Clustering of the sites resulted in four groups of assemblages, i.e. those of peatlands, open environments, forest meadows and forests. The average number of species in the groups varied from 7 in peatlands to 13 in open environments, whereas the average density of individuals was highest in open environments and lowest in forests. The groups differed with respect to dominance, species diversity, and the number of species with a clear habitat preference. Peatland assemblages were the most homogenous ones. A principal component analysis (PCA) indicated three main trends in the variation of butterfly abundance: an affinity of species to either forest environments, open environments, or peatlands. Based on these trends and their habitat preferences, the species were considered woodland, grassland and peatland species, respectively. A hypothesis about the historical formation of the present butterfly fauna in the study area is presented.

**Key words.** Butterfly communities, boreal forest zone, habitat preferences, multivariate analysis.

## Introduction

Butterflies are one of the best-known groups of Lepidoptera in the mid-taiga subzone of Russian Karelia. Studies have mainly been carried out, however, before the 1950s and have been reported in the form of simple species lists (e.g., Günther 1896; Möberg 1925; Lahtivirta 1939; Kaisila 1944, 1945; Karvonen 1945). Only Kaisila (1947) and Kozhantshikov (1958) generalised from their data and considered the ecological aspects of butterflies in detail. Recent lists, still few, have been annotated more precisely (Kozlov 1983; Kutenkova 1986, 1989).

According to available data, a total of 85 butterfly species has been recorded in the region. The species composition of the fauna is fairly similar to the well-documented fauna of Finnish Karelia, comprising 89 species (Saarinen *et al.* 2002). However, with regard to Russian Karelia we have scant information about the distribution and abundance of individual species as well as about the composition and the structure of local assemblages. In addition, changes in the butterfly fauna during recent decades and the present status of many species are not known (Ivanter & Kuznetsov 1995; Kotiranta *et al.* 1998).

We investigated butterflies at two adjacent localities in the Onega Lake area in order to partly fill this gap in our knowledge. This biogeographical province offers two advantages for evaluating the present status of the butterfly fauna in the middle taiga of Russian Karelia. On the one hand, a relatively mild climate in the Lake Onega

region allows some species to penetrate further north due to favourable conditions for reproduction. Hence, the butterfly fauna of the province is relatively rich in species. On the other hand, because of the strongly broken relief with its frequent alternation of ridges and valleys and the long-term traditional forest exploitation and agricultural practices, the landscape of the Onega Lake area is characterised by a high diversity of environments at a small spatial scale, including all major butterfly habitats in the mid-taiga subzone of Russian Karelia.

## Methods

The study area was situated on the north-western coast of Lake Onega (Fig. 1). The landscape of the region is made up of forests (60% of the area, with a predominance of Scots pine (*Pinus sylvestris*) in the tree cover), lakes and rivers (20%), open and forested bogs and mires (15%) and cultivated fields, meadows and pastures (5%) (Volkov *et al.* 1990; Gromtzev 1993). The annual mean temperature is +2.1 °C and the monthly means range from +16.8 °C in July to -10.9 °C in February (Romanov 1961).

Butterfly assemblages were studied in two nearby localities, Konchezero (1992–1993) and Kivach (1995–1996). All accessible butterfly habitats in both areas were visited before the field studies commenced and a total of 111 sampling sites (Table 1) were selected randomly. Based on the plant associations, i.e. dominant and subdominant species and relative abundance of indicators of humid and shady conditions, the sites were grouped according to the classification used by Ramenskaya (1958) and Yakovlev & Voronova (1959). The location of each site was also taken into consideration. The groups were as follows. Peat bogs and mires were oligo- and mesotrophic with semi-open or open vegetation. Tree cover was mostly dominated by Scots pine and the ground layer was comprised of oligotrophic shrubs (*Ledum palustre*, *Chamaedaphne calyculata*, *Betula nana*), sedges and herbs. Dry pine forests were dominated by Scots pine in the tree cover, and by *Cladonia* spp., *Vaccinium vitis-idaea* and *Calluna vulgaris* in the ground layer. Humid pine forests exhibited conditions varying from moderately dry to humid and the composition of the tree



**Fig. 1.** The biogeographical provinces of Karelia (Ahti *et al.* 1968) and the location of the study area (black dot). Middle taiga subzone: Ik = Isthmus karelicus, Ka = Karelia australis, Kl = *K. ladogensis*, Kb = *K. borealis*, Kol = *K. olonetsensis*, Kon = Karelia onegensis, Kton = *K. transonegensis*. Northern taiga subzone: Kpor = *K. pomorica orientalis*, Kpoc = *K. p. occidentalis*, Kk = *K. keretina*.

**Tab. 1.** The combined sampling data in ten site groups. Symbols are as follows: MIR= Peat bogs and mires, DPF= Dry pine forests, HPF= Humid pine forests, HBF= Humid birch forests, HAF= Humid aspen forests, SFM= Swampy forest meadows, HFM= Humid forest meadows, DFM= Dry forest meadows, DOM= Dry open meadows, RDS= Roadsides. For definition of vegetation types see Methods section.

Groups	Sites	Number of transects			SD	Counts (total)	Number of species	Number of individuals
		total	range	mean				
MIR	16	47	1–12	2.9	2.6	282	21	900
DPF	12	33	1–5	3.3	2.2	198	14	93
HPF	16	42	1–4	2.6	1.1	252	41	543
HBF	8	19	2–3	2.4	0.5	114	19	89
HAF	5	15	2–5	3.0	1.2	90	16	62
SFM	7	16	1–7	2.3	2.2	96	28	355
HFM	12	27	1–6	2.3	1.7	162	32	353
DFM	15	21	1–3	1.4	0.7	126	26	347
DOM	14	19	1–3	1.3	0.6	114	30	618
RDS	6	20	3–4	3.3	0.5	120	36	472
Total	111	259	1–12	2.6	0.9	1,554	50	3,832

cover varied from pure pine forests to mixed forests with a high abundance of shrubs. The ground layer vegetation varied substantially, but mosses (*Pleurozium* spp., *Hylocomnium* spp.) and *Vaccinium myrtillus* constantly prevailed in the plant associations. There were some meadow plants, but unlike the situation in forest meadows these species did not form typical associations. Humid birch forests were characterised by a predominance of birch (*Betula* spp.) and small numbers of Scots pine and spruce (*Picea abies*) in the tree cover, but aspen (*Populus tremula*) and several shrubs, such as *Rhamnus frangula*, *Rosa* spp. and *Lonicera* spp., were common in these sites. *Vaccinium myrtillus*, *Calamagrostis arundinacea*, *Deschampsia flexuosa* and some forest herbs were abundant in the ground layer. Humid aspen forests had only a small number of trees other than aspen in the tree cover. The ground layer was similar to that of humid birch forests, but species adapted to shady conditions, such as *Paris quadrifolia* and *Milium effusum*, were more common. Swampy forest meadows were dominated by *Carex nigra*, and the ground layer included common species adapted to humid conditions, such as *Agrostis canina*, *Carex canescens*, *Cirsium palustre* and *Viola epipsila*. Humid forest meadows were characterised by an unevenness of species composition and density of vegetation. The dominant species were *Alchemilla* spp., *Trollius europaeus* and *Filipendula ulmaria*. Typical plant species of swampy and dry meadow associations were distributed in small fragments along the humidity gradient. Dry forest meadows were characteristically patchy in regard to the structure of their vegetation and dominated by *Agrostis capillaris* or *Nardus stricta*. The species adapted to dry conditions, such as *Festuca ovina*, *Knautia arvensis* and *Hieracium umbellatum* were commonest in plant associations. Dry open meadows were similar to dry forest meadows, but were situated in an open arable landscape. Sites were usually bordered by lines of bushes along

drainage ditch banks, and plant associations were spotted with ruderal and weed vegetation. Roads represented both stable and open dry habitats with a predominance of meadow plants, and overgrowing habitats with bushes and forest plants.

Butterflies were studied using the transect count method (Pollard & Yates 1993). All transects were 150 m long and 3 m wide. The number of transects at each site, varying from 1 to 12, was determined by the size of the site and the heterogeneity of the vegetation structure. In the forests, only semi-open areas, such as sparsely wooded or treeless glades and tracks, were censused as boreal butterflies avoid areas with closed canopy.

Transects were studied over two seasons in each locality. The season was divided into three periods; the first was between late May and late June, the second in July, and the third one between mid-August and mid-September. Each transect was censused once in a period, and all butterflies seen within the boundaries of the route were counted. Counts were conducted between 10:00 and 15:00 local time if weather conditions were satisfactory. A transect was not censused if the temperature was lower than +18 °C, or if sunshine prevailed for less than 70% of the time, or the wind speed exceeded level three (>5.4 m/s) on the 12-point Beaufort scale.

A butterfly assemblage was defined as all species found in the site. Before any analyses were made, the data from Konchezero and Kivach were combined and the number of individuals per site was adjusted to individuals per ha. Since the species density data contained many zeros, Euclidean-based methods (e.g., *k*-means clustering and PCA) could not be used without prior transformation of the data. We applied the Chord transformation to the species data (Legendre & Gallagher 2001). The assemblages were first classified using *k*-means clustering and the resulting groups were compared by means of the species composition, the total density, the species richness and diversity, the dominance and the differences in the composition of assemblages and the number of species with a habitat preference. The species richness of butterfly assemblages was determined using rarefaction (Smith & van Belle 1984). Diversity and dominance were examined using Shannon and Berger-Parker indices (Magurran 1988), whereas compositional differences between the assemblages were evaluated using Euclidean distance. Diversity, dominance and distance between the groups were compared using ANOVA. The habitat preference of each species was based on the hypothesis that a species has the highest abundance in the most favourable habitat. The *G*-test was used for the examination of two null-hypotheses: 1) Individuals of species A are distributed evenly across all habitats. The absence of significant differences between even and actual distribution (*G*-test,  $G < 7.81$ ,  $df = 3$ ,  $p > 0.05$ ) was interpreted as non-significant habitat preference. 2) The highest abundance of species A does not differ from abundances in the other habitats. The other habitats, where the number of individuals did not differ significantly from the highest (*G*-test,  $G < 3.84$ ,  $df = 1$ ,  $p > 0.05$ ), were also classified as preferred by the species. The species density table was not appropriate for the analysis, as the species with the highest density of less than 3 individuals per hectare indicated an even distribution across the habitats. Thus, we used actual numbers of individuals, which were adjusted to equal the total square of the transects in all habitats. The proportion of sites occupied by the species indicated its degree of localisation.

Trends of structural variation in the groups of butterfly assemblages were studied by principal component analysis (PCA). The factor loadings estimate the participation of each assemblage in the separation of species along the principal component. The eigenvalue is a measure of this separation. The participation of the principal components with eigenvalues  $<1$  were equated to zero in the separation. Signs and values of the factor loadings were used for interpreting the ecological sense of the principal components. If the value of the factor loading was  $<0.7$ , it was not regarded as significant (Jeffers 1978). In accordance with the trends, the species were relegated to environment groups based on their habitat preference.

## Results

The transect count data consisted of 3,832 individuals representing 50 species. The three most abundant species were *Callophrys rubi*, *Brenthis ino* and *Pieris napi*, which accounted for 24% of all individuals. In addition, 12 species were found outside the study sites: *Carterocephalus palaemon*, *Papilio machaon*, *Pieris brassicae*, *Pontia daplidice*, *Colias hyale*, *Satyrrium pruni*, *Glaucopteryx alexis*, *Issoria lathonia*, *Vanessa atalanta*, *Vanessa cardui*, *Nymphalis io* and *Nymphalis antiopa* (nomenclature after Kullberg et al. 2002).

According to *k*-means clustering of butterfly assemblages the type of vegetation was not decisive for the structure of the assemblage, since assemblages in habitats with different plant associations could be similar and vice versa. The clustering indicated four large groups of assemblages (Table 2), after rejection of two mire assemblages which formed independent clusters and were thus excluded from all further considerations. The groups were as follows: 1) The peatland group included assemblages of both bogs and mires and adjoining dry pine forests. 2) The open environment group included assemblages of dry open meadows, roadsides and forest habitats situated near open environments. 3) The forest meadow group included assemblages of forest meadows and treeless glades with rich vegetation, located apart from open environments. 4) The forest group included assemblages of sparsely wooded glades, tracks and small overgrown forest meadows. Means of pairwise Euclidean distances within groups indicated that the peatland group was the most homogenous one (Table 3). The differences between groups were all significant (one-way ANOVA:  $F=39.75$ ,  $df=3$ , 1485,  $p<0.0001$ ).

**Tab. 2.** Clustering of the butterfly assemblages. Given are numbers of assemblages as represented in the four groups revealed by *k*-means clustering. Two outlier assemblages at the MIR-sites were excluded from the analysis.

	MIR	DPF	HPF	HBF	HAF	SFM	HFM	DFM	DOM	RDS	total
Peatlands	14	5	-	-	-	-	-	-	-	-	19
Open environments	-	1	3	-	-	-	3	7	14	5	33
Forest meadows	-	2	4	2	-	4	8	5	-	1	26
Forests	-	4	9	6	5	3	1	3	-	-	31

**Tab. 3.** The number of species, the density of individuals, and the similarity, species diversity and dominance in the four groups of butterfly assemblages. The differences between groups were significant in each category (one-way ANOVA, see Results section). \* number of pairwise Euclidean distances to be compared.

	Peatlands n=19 *n=171	Open environments n=33 *n=528	Forest meadows n=26 *n=325	Forests n=31 *n=465
Number of species observed				
mean	7.2	12.9	10.2	7.5
SD	2.8	3.9	3.8	3.4
Individuals per hectare				
mean	49.7	88.2	55.2	34.8
SD	45.9	37.5	26.5	28.7
Euclidean distance*				
mean	0.128	0.146	0.155	0.158
SD	0.029	0.028	0.035	0.036
Shannon index (H')				
mean	1.72	2.27	1.99	1.60
SD	0.30	0.29	0.39	0.47
Berger-Parker index (d)				
mean	0.31	0.22	0.29	0.42
SD	0.07	0.06	0.11	0.19

In the four groups the average number of species was highest in open environments and lowest in peatlands (one-way ANOVA:  $F=16.86$ ,  $df=3$ ,  $105$ ,  $p<0.0001$ ). According to rarefaction curves, the species richness was rather equally high in open environments and forest meadows, and equally low in forests and peatlands (Fig. 2). The average density of individuals varied from 34.8 individuals  $ha^{-1}$  in forests to 88.2 individuals  $ha^{-1}$  in open environments (one-way ANOVA:  $F=13.46$ ,  $df=3$ ,  $105$ ,  $p<0.0001$ ). Species diversity was highest in the assemblages of open environments and lowest in forest assemblages (one-way ANOVA:  $F=19.19$ ,  $df=3$ ,  $105$ ,  $p<0.0001$ ).

Peatland assemblages were dominated by *Boloria aquilonaris*, *Albulina optilete* and *Callophrys rubi*; those of open environments by *Pieris napi*, *Aphantopus hyperantus* and *Nymphalis urticae*; those of forest meadows by *Erebia ligea*, *Brenthis ino* and *Gonepteryx rhamni*; and those of forests by *Brenthis ino*. The Berger-Parker index indicated the highest dominance in forest assemblages. The differences between groups were all significant (one-way ANOVA:  $F=7.89$ ,  $df=3$ ,  $105$ ,  $p<0.0001$ ).

A total of 47 species exhibited a significant habitat preference as defined in the Methods section (Table 4). Five species were observed only in peatlands (*Boloria eunomia*, *B. freija*, *Coenonympha tullia*, *Erebia embla*, *Oeneis jutta*). Others were exclusive to open environments (*Pieris rapae*, *Lycaena hippothoe*, *Coenonympha glycerion*) or forest (*Pararge aegeria*, *Erebia euryale*). There were 30 species with a preference for a single habitat type. The number of species showing distinct habitat preferences varied from 7 in forests to 23 in open habitats. The highest localisation of the populations across the environments was recorded for *Pyrgus malvae*, *P. alveus*,

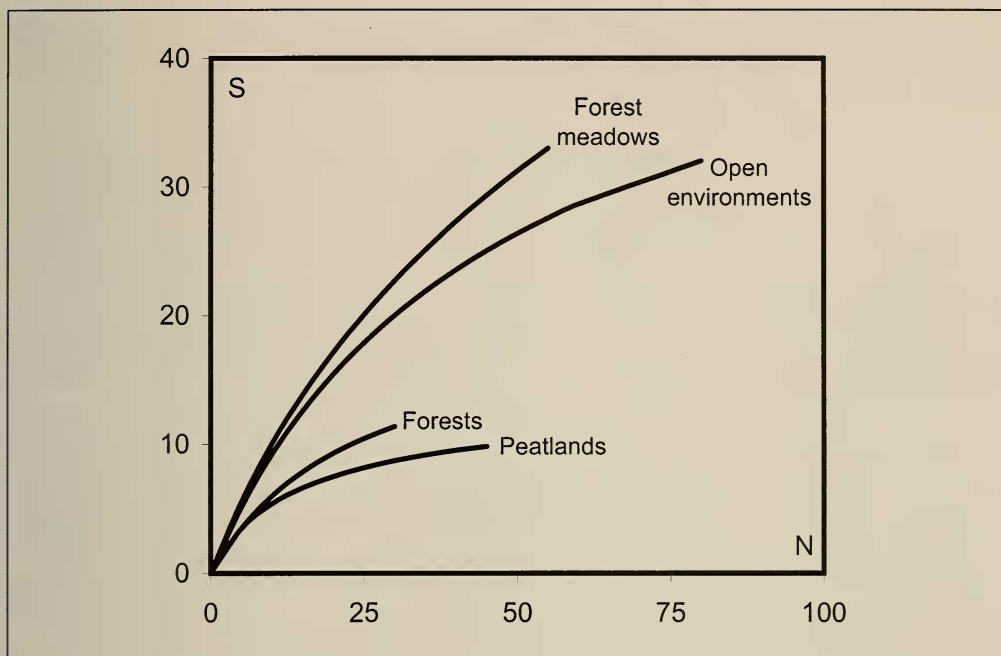


Fig. 2. Rarefaction curves for the four groups of butterfly assemblages. S – expected number of species, N – number of individuals (sample size).

*Aricia eumedon*, *Boloria freija*, *B. titania*, *Euphydryas maturna*, *Erebia euryale*, *Coenonympha glycerion*, *Pararge aegeria* and *Lasiommata petropolitana*.

PCA produced two significant components which together accounted for more than 75% of the data variance (Table 5). The first component included significant factor loadings for assemblages of forests and forest meadows. Along the second axis, the butterfly assemblages of open habitats contrasted with those of peatlands. Thus, PCA results indicated three main trends in the variation of butterfly abundances: an affinity of species to forest environments, open environments, or peatlands (Fig. 3).

## Discussion

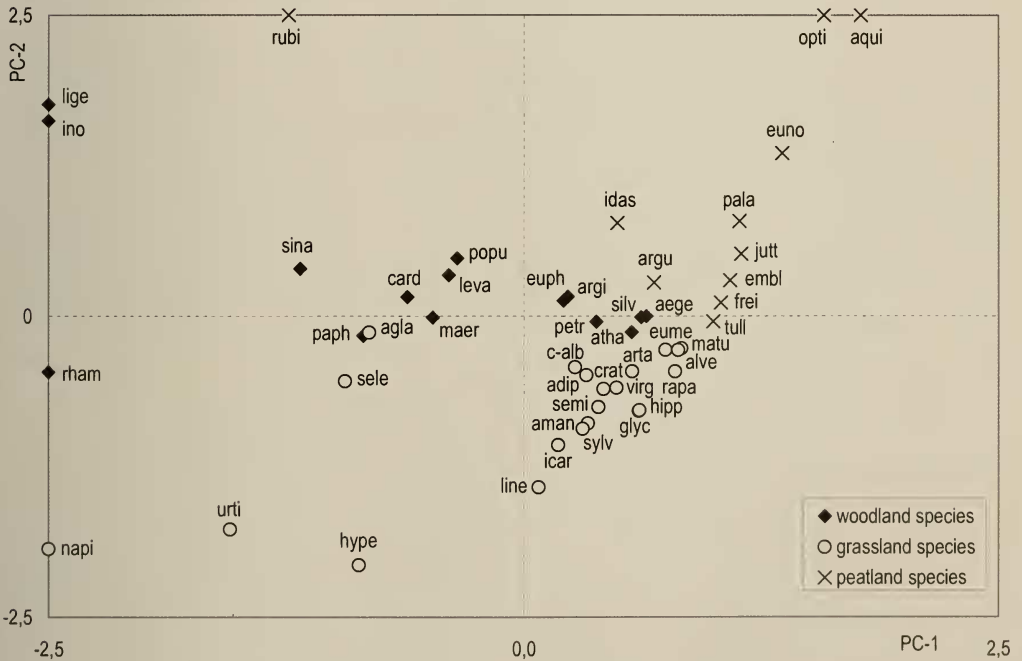
A total of 62 species found in the two localities correspond to 71% of all species known from Russian Karelia. Only 12 species previously recorded from the Onega Lake area in Karelia were not observed. Of these, some have a more or less disjunct distribution in Russian Karelia (*Pyrgus centaureae*, *Lycaena helle*, *Aricia nicias*, *Argynnis niobe*, *Boloria frigga*, and *Coenonympha pamphilus*), while others are known from a few populations on the shores or islands of Lake Onega (*Hesperia comma*, *Parnassius mnemosyne*, *Maniola jurtina*, and *Maniola lycaon*) or as single finds in the area (*Colias crocea*, *Lycaena phlaeas*) (Kaisila 1947; Kozlov 1983; Kutenkova 1989). In general, only a few local or migrant species distinguish the provincial fauna from the faunas of adjacent areas (Peltonen 1947; Kozhantshikov 1958; Sotavalta 1987).





**Tab. 5.** Eigenvalues of the principal components and the factor loadings (values >0.7 in **bold**) of the four groups of butterfly assemblages.

Principal component	PC-1	PC-2
Eigenvalue	1.846	1.177
Cumulative % variance explained	46.2	75.6
Peatlands	-0.275	<b>1.000</b>
Open environments	0.508	<b>-0.823</b>
Forest meadows	<b>1.000</b>	0.240
Forests	<b>0.924</b>	0.490



**Fig. 3.** PCA ordination diagram of butterfly species (indicated as four-letter codes derived from species epithets) along the first two principal components. Seven species printed exactly upon the borders of the diagram are due to a reduction in the graphic area. Three groups (collapsing forests and forest meadows, see Table 5) were defined according to the highest densities of the species (Table 4), excluding three species with no preference for any of the environment groups as they emerged from a *k*-means clustering.

The abundance of the majority of butterfly species in the study area was similar to that in the Onega Lake area in the 1940s (Kaisila 1947) as well as in SE Finland in the 1990s (Marttila *et al.* 2001). The most abundant species included *Pieris napi*, *Gonepteryx rhamni*, *Callophrys rubi*, *Brenthis ino*, *Nymphalis urticae*, *Aphantopus hyperantus* and *Erebia ligea*. In contrast, *Papilio machaon*, *Pieris brassicae*, *Nymphalis antiopa* and *Boloria euphrosyne* had a surprisingly low abundance in the study area. Species with relatively discrete populations (e.g., *Pyrgus alveus*, *Boloria titania*, *Boloria freija*, *Erebia*

*eurycle* and *Pararge aegeria*), in addition to other local species, are probably the most vulnerable in the provincial fauna, although some had rather high abundances in particular sites.

Butterflies in the Onega Lake area are concentrated in more or less open habitats within forests, including peat bogs and mires, and non-cultivated areas in arable landscapes. The average density of butterflies was rather similar in comparison to other studies carried out in the middle and southern taiga. In a pine bog in SE Finland, Väisänen (1992) reported 58 individuals ha<sup>-1</sup>. In arable landscapes in Finnish and Russian Karelia, 45 to 101 individuals ha<sup>-1</sup> were recorded on field boundaries (Saarinen & Jantunen 2002). In addition, the lists of dominant and common species commonly coincided. Some differences may be due to the fluctuation of butterfly populations between the years. In addition, the number of species and the total density in the assemblages varied substantially. The phenomenon is a consequence of two reasons. Firstly, the assemblages with varying number of species and total density were united into a few groups according to their similarity of structure. For example, the highest variation in total density was recorded in the peatland group, which was an amalgamation of more abundant assemblages of peat bogs and mires and less abundant assemblages of dry pine forests. Differences in their structure, however, were the lowest among the four groups of assemblages. Secondly, the quality of the environment for species may differ even between similar habitats. This effect, however, is impossible to assess without detailed investigation of many factors. No doubt the most important ones are the presence of a sufficient number of food plants for larvae and adults, and a favourable meso- and microclimate (e.g., Holl 1995; Dover *et al.* 1997). It is also necessary to take into consideration the position of a habitat in the surrounding landscape matrix and its degree of isolation. Some species are mobile and counts may reflect the attraction of individuals to nectar sources (Pollard 1977). For example, the flowering of *Potentilla palustris* resulted in a high density of *Boloria aquilonaris*, while the concentration of another abundant species, *Callophrys rubi*, was a consequence of the flowering of *Chamaedaphne calyculata* and *Ledum palustre*. Hence the presence and the density of butterfly species may strongly depend on the abundance of these plants in the habitat. In the majority of cases, however, the number of species and the high density of individuals did not result from trophic migration of adult butterflies, but seems to indicate the most favourable habitats. Butterfly movements are commonly short (e.g., Scott 1975; Ehrlich 1984; Thomas 1984) and the migration of individuals to suitable habitats is in most species not a mass phenomenon (e.g., Dempster 1991; Shreeve 1992; Hanski & Kuussaari 1995). The intensity of migration may depend on distance and the availability of natural barriers between habitats. The effect of a possible concentration of butterflies in small areas within the boundaries of one site was reduced by using several transects spread evenly across each site.

The structure of the assemblages was characterised by indices of species diversity and dominance, which are inversely correlated with each other; the higher the diversity, the lower the dominance. Low species diversity and higher dominance in the peatland assemblages may be explained by extreme levels of humidity and specific plant associations, while forest assemblages were impoverished by the most shady

conditions and the poverty of ground layer vegetation. Consequently, these habitats were unsuitable for most species, and those observed usually appeared in small numbers. In contrast, higher species diversity and low dominance in the assemblages of open environments indicated that habitats are suitable for the majority of species in the study area.

The most important differences between the assemblages are due to a great extent to the habitat-specific species. In general, our results further endorsed previous knowledge of the habitat preferences of butterflies in the boreal zone (Marttila *et al.* 2000).

Based on the analyses of the structural variation we conclude that the peatland group is distinct from the rest. This fauna is mainly composed of tyrphobiont and tyrphophilous species. Due to their close association with peatlands, the ability of the latter in regard to transition to other habitats is extremely limited (Mikkola & Spitzer 1983). Most butterfly species, however, are able to utilize different habitats, even though in different abundances. Thus, the assemblages from forest and open environments did not differ significantly with respect to species composition, but abundances of the species varied substantially. In general, the separation of the fauna into woodland and grassland species is a result of the anthropogenic transformation of a once continuous coniferous forest cover. Prior to human alteration of pristine landscapes, species preferring open habitats apparently existed as small populations in forest openings, such as glades and unforested bedrock, as well as on shore meadows. Later on, these species moved into anthropogenic meadows and due to increasing numbers of individuals, they have become noticeable elements of the fauna. The assemblages of forest meadows can be considered as a transitional stage to open meadow assemblages. This standpoint conforms to Nitzenko's (1969) hypothesis about the origin of meadow plant associations in the middle taiga. Due to the trophic specialisation of butterflies, we may suppose that butterfly species followed their host plants on to the meadows. The increase in numbers of individuals was probably caused by a gradual increase of food resources, with many herbs finding more favourable conditions in open habitats. In addition, some butterflies might penetrate from southerly areas and so form resident populations in suitable sites. The formation of a butterfly assemblage in meadows was accompanied by an increase in species diversity, as numerous grassland species appeared in addition to abundant and common woodland species. The overgrowing of meadows leads to the impoverishment of the species composition and a reduction in total abundance in the butterfly assemblage. This is illustrated in deciduous forests in the taiga zone, which according to Ramenskaya (1958) are a result of the overgrowth of meadows due to lack of management. We predict that the structure of any local fauna in the middle taiga is defined by the proportion of peatland, forest and open environments in the area and the heterogeneity of the habitats available in the landscape matrix.

#### Acknowledgements

The authors gratefully acknowledge Ernest V. Ivanter, Sergei D. Uzenbaev, Andrei V. Korosov and Nadezhda N. Kutenkova for their support and help in the study. We are also indebted to Leigh Plester and two anonymous referees for valuable comments on the manuscript.

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